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PERIODICITY IN THE PRODUCTION OF THE SEXUAL CELLS OF *DICTYOTA DICHOTOMA*[1]

CONTRIBUTIONS FROM THE BOTANICAL LABORATORY OF THE JOHNS HOPKINS UNIVERSITY, No. 6

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(WITH TWO CHARTS)

The antheridia of *Dictyota dichotoma* (Huds.) Lamour. were described in 1855 (**1**), but the motility of the spermatozoids was not discovered until 1896 (**2**).

In 1898 WILLIAMS (**3**) stated that the sexual cells of this alga are produced in fortnightly crops bearing a definite relation to the tides, and suggested that illumination is the factor determining the time of fruiting. In an excellent paper on the cytology of the gametophytic generation (**4**) the same author added a few details to his previous statements, and in 1905 (**5**) he gave a full account of the periodicity of Dictyota on the north coast of Wales, near Bangor, and discussed the factors which may determine this behavior. He also recorded a similar periodicity in this alga at Plymouth, England. At both places the time of production of the sexual crops bears a definite relation to the spring tides. The spring tides are, of course, those of greatest range, having the highest floods and the lowest ebbs, and occur every two weeks, about the times of the new and full moons. The neap tides are those of least range, having the lowest floods and the highest ebbs, and occur between the springs. A summary of records taken at Bangor for seven years shows that at this place the sexual crops of *Dictyota dichotoma* are generally initiated several tides before the least neap, and liberated from three to five tides after the greatest spring. They thus extend through parts of two sets of spring tides.

In his discussion of the factors which may regulate the periodicity, WILLIAMS assumes that the determining factor is one that varies with the alternation of spring and neap tides, and is most marked at the greatest spring tides. The effect of aeration, temperature, pressure, and light is considered. The first three are deemed negligible because plants in different situations subjected to different conditions in these respects show the same behavior in fruiting. Light, then, is the remaining condition which, with the alternation of spring and neap tides, varies most for the plants of all situations, and this is believed to be the determining factor for the following reasons. (1) At Bangor the development of each crop is rapid at first, when there is comparatively little water over the plants at low tide and much light is obtained. The development is retarded with the approach of neap tides when the light is weak, and is accelerated by the following spring tides when the available light again becomes strong (*chart 1*). (2) Whether liberation shall occur on the third or fifth tide after the greatest spring tide depends on whether the preceding spring tides have been great or small, thus giving more favorable or less favorable light conditions for the rapid development of the early stages. (3) The length of time taken by any crop to pass from initiation to liberation is directly proportional to the number of days intervening between one set of spring tides and the next; in other words, to the number of days when the available light is weak. (4) During October and November the light becomes less intense at the low water of spring tides, and both initiation and liberation are delayed several tides. (5) At Plymouth, England, the crops seem to be produced wholly within one set of spring tides, and the time of liberation seems to be determined by the height of the tides during development. The light is less advantageous at the low water of spring tides, and liberation does not occur until seven to twelve tides after the greatest spring.

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[1] An abstract of this paper was presented before Section G of the A. A. A. S., New York City, December 31, 1906.

These facts seem to show a causal relation between the amount of available light and the time of fruiting, but a single experiment tends to make this conclusion less certain. Two sexual plants of Dictyota were brought into the laboratory in October and left undisturbed during the winter. When examined the following April, they produced three crops at fortnightly periods, although they had been removed from the alternating influence of the tides for six months. WILLIAMS therefore concludes that "periodicity of the sexual cells is an hereditary character and consequently may be expected to manifest itself in seas and habitats where there are no tides. At the same time, the sexual cells are so responsive to changes in the amount of illumination that the time of their development in seas where there are tides is regulated by the increased illumination obtained during the low water of spring tides" (**5**, p. 548).

During a stay at the laboratory of the Bureau of Fisheries at Beaufort, N. C., the past summer, a record was kept of the fruiting of the sexual plants of *Dictyota dichotoma*, together with observations on the tides and the conditions of growth. The following facts were observed. (1) The sexual cells were produced in regular periodic crops. (2) The time of the production of these crops bore a definite relation to the tides. (3) The crops were borne at monthly instead of fortnightly intervals, appearing only at alternate spring tides. (4) Rudiments of sexual organs were first observed on the day of, or the day before, the greatest spring tide, instead of a few days before the least neap as at Bangor. (5) The time taken for the development of an entire crop was about eight or nine days, instead of twelve to seventeen days. (6) General liberation occurred six days after the greatest spring tide, instead of two to five days. (7) Differences in the height of different sets of spring tides had no effect on the time of liberation or the time taken for the development of an entire crop. Thus, the August crop was liberated six days after the greatest spring tide, the preceding ebb tides having been the lowest observed during the summer. The October crop was liberated at the same interval, although the tides for nearly a month previous had been exceptionally high at both ebb and flood. (8) Differences in the time intervening between one set of spring tides and the next had no effect on the time of initiation of rudiments or of liberation of gametes. Although the number of days between one spring tide and the next varied from twelve to eighteen, rudiments were always first observed about the day of the greatest tide, and liberation always occurred six days after the greatest tide of each alternate set of springs.

A comparison of the record of a single crop at Beaufort, beginning with the day when rudiments of sexual organs were first observed, with a similar record for a crop on the coast of Wales, will best illustrate the difference in development (*charts 1* and *2*). This record is followed in each case with male plants, and the numbers given are

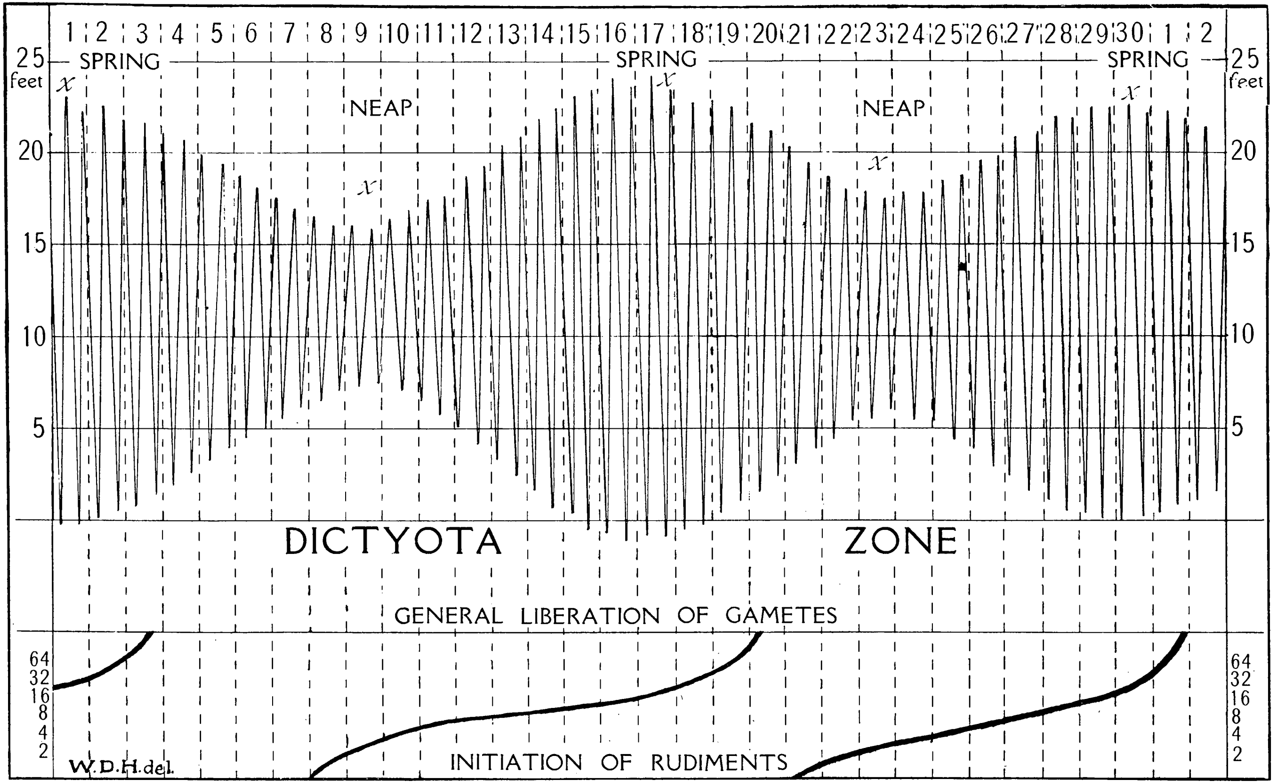

CHART 1.—Tidal relations at Bangor, Wales, for thirty-two days, showing great tides and two crops of Dictyota.

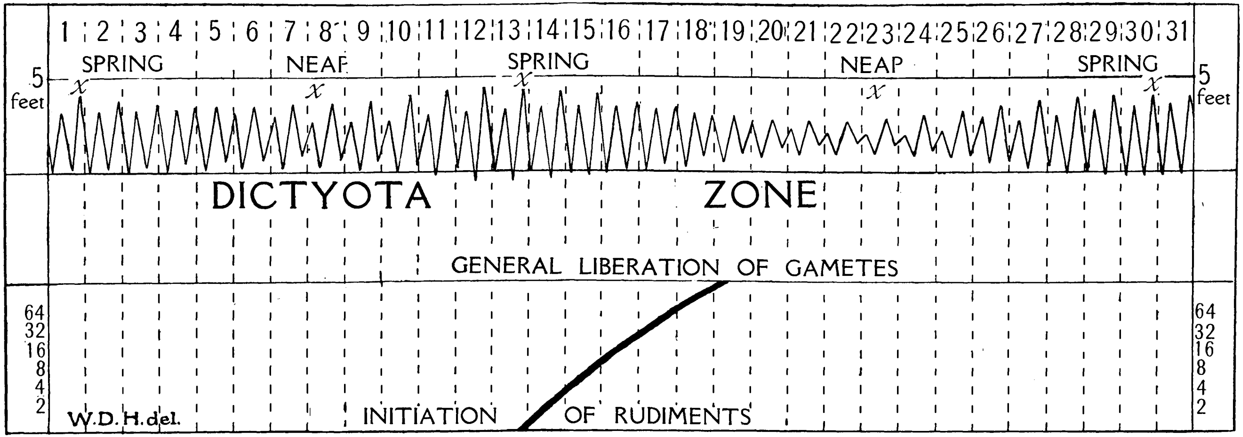

Chart 2.—Tidal relations at Beaufort, N. C., for thirty-one days, showing slight tides and only one crop of Dictyota.

The tide records are taken from the Tide Tables for 1906 of the U. S. Coast and Geodetic Survey. While wind and other factors may cause any tide to vary from the heights given at either Bangor or Beaufort, the figures show the general course of the rise and fall at the two places. The curves showing the development of Dictyota at Bangor are adapted from Williams (**5**, p. 559). The two charts are drawn to the same scale. The zig-zag lines show the rise and fall of the tide and the heights of the water in relation to the Dictyota zone. The curved lines show the development of the sexual crops of Dictyota for the respective periods with their relations to the tides. The numbers opposite the crop curves indicate the number of cells seen in the surface-view of each antheridium.

those of cells seen in the surface-view of each antheridum. The actual number of cells in each antheridium is much greater. These show as follows:

	Beaufort	Bangor
1st day.......	Undivided rudiments	Undivided rudiments
3d day.......	8–16 cells	" "
4th day.......	32–64 cells	" "
5th day.......	64 cells	" "
6th day.......	General liberation	
7th day.......	Liberation from belated sori	2–4 cells
10th day.......		Many 64 cells
12th day.......		General liberation
13th day.......		Liberation from belated sori.

In addition to this difference is the fact that the records taken make it probable that every crop produced during the fruiting season at Beaufort was similar in development to the one described, while at Bangor there is considerable difference in the development of different crops. The cause of these differences in the fruiting of the plants on our coast and on the coasts of Wales and England is not apparent. A comparison of the tides at the different localities, however, is of interest in this connection (**6**) (*charts 1* and *2*).

The average range of the tide is: near Bangor, Wales, 17.9 feet; at Plymouth, England, 11.5 feet; at Beaufort, N. C., 2.8 feet. The average difference in the height of low water at spring and neap tides is: near Bangor, Wales, about 5.7 feet; at Plymouth, England, about 3.4 feet; at Beaufort, N. C., 0.5 foot. We are still unable to say whether these differences will explain the difference in behavior, or whether this is due to some other, possibly ancestral, cause.

It is possible that the Dictyota occurring at Beaufort is a different species from that found at Bangor or Plymouth. To determine this, a specimen was sent to Mr. Frank S. Collins of Malden, Massachusetts, who verified the identification, referring it to *D. dichotoma.* In spite of the morphological resemblance, however, it is possible that the Beaufort form is a different physiological species, and this can be determined only by means of cultures. The final test can be made only by growing some of the Bangor plants at Beaufort and *vice versa.* It is hoped that this can be done at some future time.

The explanation of this periodicity is not apparent. Although the behavior of this alga at Bangor and Plymouth may be explained by the assumption that illumination is the determining factor, the facts observed at Beaufort indicate that for the plants of this region, at least, some other explanation must be sought. That the time of fruiting is determined to some extent by the tides is indicated by the very exact relation which this bears to the tides. That illumination is not the determining factor is indicated by the facts that fruiting occurred only on alternate spring tides, that differences in the amount of light as determined by the state of the weather and the heights of different sets of spring tides had no effect on the time of fruiting, and that the differences in light conditions to which individual plants are subjected are greater than those differences to which all the plants are subjected because of differences in the height of water at spring and neap tides.

As was mentioned above, the average difference in the height of low water at Beaufort at spring and neap tides is only 0.5 foot. As the difference in the depths at which individual plants grow is at least six times as great as this, the difference in the amounts of light received by different plants at any instant is greater than the differences in the amounts of light received by any one plant at low water of spring tide and at low water of neap tide. And yet all the sexual plants observed in all situations fruited at the same time. It may be urged that the sexual plants are sensitive, not to the actual amount of light, but to the maximum intensity, and that this occurs at the time of the spring tides for the plants of all situations. But the same reasoning applies to all the other factors which are influenced by the tides—such as aeration, pressure, etc.— so that there is no more reason on this ground to ascribe the behavior to the light than to any one of the other factors.

One observation is interesting in this connection. A female plant was brought into the laboratory August 11 and placed in a covered jar of sea-water near a window. As is often the case when *Dictyota dichotoma* is subjected to unfavorable conditions, proliferations were formed from the margin of the thallus. When examined October 6, most of the plant had died, but several proliferations were still alive, and these showed sori of uniform age only slightly less advanced than those on plants growing in the harbor. In this case the entire plant had been removed from alternating conditions (except those of day and night) for nearly two months, and the sori were borne on proliferations produced while the plant was in the laboratory, consequently on parts of the thallus whch had never been subjected to alternating conditions. This result is similar to one obtained by WILLIAMS (**5**, p. 547), but goes one step farther in showing that the periodicity is transmitted to new structures formed from the original plant, even when these are not subjected to alternating conditions. These proliferations were, of course, produced by the protoplasm of the parent plant; it still remains to be seen whether the periodic habit can be transmitted through the protoplasm of the egg.

A few observations were made at Beaufort in the summer of 1905, but no satisfactory records were obtained. The observations made, however, indicate that the behavior of the sexual plants was like that observed during the past summer.

Many specimens of several species of Dictyota have been obtained from two localities in Jamaica. Among these are four sexual plants—two male and two female—collected by the author at Port Antonio, April 13, 1906, and eight sexual plants—two male and six female—collected by Mr. I. F. LEWIS at Port Morant, July 16, 1906. Although this material is too scanty to warrant a conclusion, it is interesting to note the direction in which the evidence points.

The specimens from Port Antonio have all the sori of about the same age, and at the same stage of development that would be expected for plants of Dictyota at Beaufort, N. C., on the same day. In the specimens from Port Morant, the male plants have all the sori of the same age, while all the female plants have sori of two ages, one set being mature, and the other being young and at a stage corresponding to that of the antheridial sori on the male plants. These sori of two ages probably represent two crops of eggs, the older of which was not shed before the younger one was produced. The age of the older crop cannot be stated with certainty, but the age of the younger crop of eggs and of the antheridial sori does not agree with the age of sori on plants collected by the author on the same day at Beaufort. They seem at about the stage of development, however, that would be expected for Dictyota at Bangor on this day. These facts indicate that, on the coast of Jamaica also, Dictyota shows periodicity in the production of sexual cells. As there are practically no tides on this coast (about six inches), this condition, if true, supports WILLIAMS' conclusion that "the periodicity of the sexual cells is an hereditary character and consequently may be expected to manifest itself in seas and habitats where there are no tides."

As the Jamaican specimens of Dictyota belong to more than one species, the facts indicate the probability that periodicity obtains throughout the genus. The apparent correspondence in the time of fruiting of the Port Antonio specimens with those of Beaufort, and of the Port Morant specimens with those of Bangor may be only a coincidence. It is certain, however, that the time of fruiting of the Port Morant specimens did not coincide with that of Dictyota at Beaufort. Evidently we need more observations before we can draw general conclusions or suggest explanations of the facts already observed.

The author is able to verify WILLIAMS' statements that light is not necessary for the escape of the sexual cells of *Dictyota dichotoma*, and that the tetrasporic plants show no periodicity.

From a single set of observations, WILLIAMS gives evidence of periodicity in "Haliseris" and suggests by inference the possibility of its occurrence throughout the Dictyotaceae. A species of Padina, probably *P. Durvillaei* Bory, is abundant at Beaufort in the same situations with Dictyota. Numerous male plants were found and these showed no evidence of periodicity, sori of all ages occurring on the same plant. It seems, therefore, that periodicity is not characteristic of all the Dictyotaceae. All the sexual plants of Padina which were examined bore only antheridia and produced these on both sides of the thallus, differing in these respects from the printed descriptions. The antheridia were numerous, being borne in sori in wide concentric rows which appeared white to the naked eye, and the sori were usually produced in regular acropetal succession.

The author expects to continue this work, but, believing the present data to be insufficient to explain this periodicity, gives the results already obtained with the hope of inducing other botanists who are favorably situated to begin a study of this form. It seems that only by observations of the fruiting and careful comparison of the conditions at a number of places for a considerable period of time can we hope to understand this striking phenomenon.

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CONCLUSIONS

1. As on the coast of Wales and England, *Dictyota dichotoma* at Beaufort, N. C., produced its sexual cells at regular intervals, bearing a definite relation to the tides.

2. The time of production of these crops, however, differs from that on the coasts of Wales and England, the crops being borne at monthly instead of fortnightly intervals.

3. The assumption that light is the sole factor determining the time of fruiting does not hold for the plants of *Dictyota dichotoma* growing at Beaufort.

4. Specimens of Dictyota from Jamaica indicate that there also the sexual cells are produced in periodic crops, and that periodicity may obtain throughout the genus. The time of fruiting, however, at least in some cases, is different from that of Dictyota at Beaufort.

5. Periodicity in the production of the sexual cells is not universal among the Dictyotaceae. A species of Padina, probably *P. Durvillaei* Bory, bears antheridial sori of all ages on the same plant.

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